ARTICLE

Bird communities and vegetation associations across a treeline ecotone in the Mealy Mountains, Labrador, which is an understudied part of the boreal forest

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Abstract: We examined the factors structuring bird communities across a complex subarctic treeline in the Mealy Mountains, Labrador, Canada. Using point counts of bird abundance in 2007 and 2008, we show that changes in vegetation driven by elevation are strongly correlated with avian community structure in this treeline ecotone system. Overall, avian diversity was higher in the forest compared with other habitat classes (krummholz, deciduous shrub, and alpine). There were strong correlations between avian diversity and vegetation richness, as well as structure, among and within habitat class in 2008. Numerous habitat types (subset of habitat class) were correlated with avian composition, although some species were clearly habitat generalists. Contrary to expectation, avian species composition was associated with physiognomy (vegetation structure) in alpine and deciduous shrub, and with either physiognomy or floristics (vegetation species composition) in krummholz and forest. Given the strong impact of elevation on vegetation and the demonstrated influence on bird communities, we note that for bird species whose near-southernmost populations are found in the Mealy Mountains, climate change is likely to have a strong negative effect if alpine tundra habitat is lost. Furthermore, forest bird species are likely to benefit from the increased tree cover as treeline moves poleward and upward.

Key words: treeline, avian species richness, vegetation volume, forest–tundra ecotone, plant community composition, boreal forest, Labrador.

Résumé : Nous avons examiné les facteurs qui structurent les communautés d'oiseaux de part et d'autre d'une limite des arbres subarctique complexe dans les montagnes Mealy (Labrador, Canada). En utilisant des dénombrements ponctuels de l'abondance d'oiseaux en 2007 et 2008, nous démontrons que les changements de la végétation associés à l'altitude sont fortement corrélés à la structure de la communauté d'oiseaux dans ce système d'écotone de limite des arbres. Globalement, la diversité des oiseaux était plus élevée dans la forêt que dans les autres classes d'habitat (krummholz, arbustes feuillus et alpin). Il y avait de fortes corrélations entre la diversité des oiseaux et la richesse de la végétation, ainsi qu'avec la structure, entre les classes d'habitat et au sein de celles-ci en 2008. De nombreux types d'habitat (sous-ensembles des classes d'habitat) étaient corrélés avec la composition d'oiseaux, bien qu'il soit clair que certaines espèces sont des généralistes en ce qui concerne l'habitat. Contrairement aux prédictions, la composition des espèces d'oiseaux était associée à la physionomie de la végétation dans les habitats alpins et d'arbustes feuillus et soit à la physionomie de la végétation ou à la floristique (composition spécifique de la végétation) dans les habitats de krummholz et forestiers. Étant donné la forte incidence de l'altitude sur la végétation et l'influence démontrée sur les communautés d'oiseaux, nous notons que les changements climatiques auront vraisemblablement un fort effet négatif sur les espèces d'oiseaux dont les populations les presque plus au sud se trouvent dans les montagnes Mealy, si l'habitat de toundra alpine disparaît. En outre, les espèces forestières d'oiseaux profiteraient vraisemblablement du couvert arboré accru découlant du déplacement de la limite des arbres vers le pôle et vers le haut. [Traduit par la Rédaction]

Mots-clés : limite des arbres, richesse spécifique des oiseaux, volume de la végétation, écotone forêt–toundra, composition de la communauté de plantes, forêt boréale, Labrador.

Introduction

Ecotones have been extensively studied in large part because of the significant influence they have on biodiversity (Risser 1995; Payette et al. 2001; Harper et al. 2005). This increase in biodiversity is often attributed to the large changes in vegetation structure over short distances or specialization at edges (Ries and Sisk 2004). Changes in vegetation at the forest–tundra ecotone (treeline), an ecotone caused by complex changes at a latitudinal or altitudinal gradient, have been extensively documented (Payette et al. 2001; Harper et al. 2011), in response to the growing concern that global

climate change may adversely affect these important areas (Grace et al. 2002). However, the impact of treeline ecotones on other key organisms like passerine songbirds remains relatively unstudied (Terborgh 1985; Archaux 2004; Lloyd et al. 2011; Kent et al. 2013), and boreal ecotone communities are especially understudied.

The influence of treelines on biodiversity is of concern in northern regions because the boreal forest is critical for the biodiversity and viability of populations of North American passerine birds (Blancher 2003; Blancher and Wells 2005). Furthermore, significant impacts of climate change are predicted to occur at boreal

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latitudes resulting in increased plant growth (infilling; Danby and Hik 2007) or increased recruitment in treeline species, and a subsequent migration of the treeline, latitudinally and altitudinally (Cannone et al. 2007; Ruckstuhl et al. 2008; Harsch et al. 2009). The potential for changes in avian distribution in response to a changing climate was suggested by Cumming et al. (2014), who showed that climate variables explained most of the deviance in abundance of boreal songbird distribution. An examination in the boreal region will broaden our understanding of the influence of ecotones on avian diversity and shed light on the influence of global climate change on these regions.

Relevant to understanding the influence of ecotones and a changing climate on passerine songbirds is the vegetation–habitat concept, considered a unifying theory in avian biology (Lee and Rotenberry 2005). Vegetation as habitat can influence avian assemblages in terms of structure (physiognomy: MacArthur et al. 1962; James and Wamer 1982; Cody 1985; Bersier and Meyer 1994) and composition (floristics: Rotenberry 1985; Bersier and Meyer 1994). Ecotones, including the treeline, provide an excellent opportunity to examine the vegetation–habitat concept because the changes in physiognomy and floristics across the treeline allow for examination of communities that may differ dramatically over short distances (<5 km). Therefore, although the debate over the relative roles of physiognomy and floristics on avian assemblages is not new, it should be re-examined in the context of global climate change and expected poleward and upward shifting treeline ecotones.

We examined avian community structure and its relationship to vegetation across a treeline ecotone in the Mealy Mountains (*Akamiuapishkua*), a highland area of south-central Labrador, Canada. This region is projected to warm by 2.05–4.32 °C over the next 80 years (Bell et al. 2008) and climate–habitat simulations show that the treeline is expected to move both poleward and upward (Loader 2007). Due to topography and edaphic factors, the treeline ecotone is complex, resulting in a highly variable deciduous shrub – krummholz zone bounded by largely contiguous forest and capped by a small amount of alpine tundra (currently less than 10% of the total area; Loader 2007). The relatively species-poor avifauna (composed of both habitat specialists and generalists) and high variation in physiognomy and floristics over a small area allowed us to test the following questions: (*i*) how do measures of avian diversity vary with elevation, vegetation richness, and vegetation structure across the ecotone and (*ii*) to what degree are elevation, floristics, and physiognomy associated with avian composition across the ecotone? Answers to these questions are critical to our ability to predict shifts in avian communities owing to climate change. Finally, we report the first systematic study on avian diversity in this rarely studied part of North America.

Materials and methods

Study area

The Mealy Mountains are the dominant highlands of southern Labrador, occupying an area of approximately 2000 km² directly south of Lake Melville (Fig. 1). Mountain summits are broad and rounded, with an elevation just over 1100 m. The highlands (above 800 m) are dominated by alpine vegetation, are surrounded by boreal forest and wetlands at lower elevations, and have been described as southernmost mountainous outliers of the High Subarctic Tundra ecoregion (Meades 1990). Local glacial and glaciofluvial deposits are conspicuous and important components of the landscape, influencing position and structure of the vegetation.

The Labrador Highlands Research Group base camp is located approximately 20 km south of Lake Melville, in an eastward trend-

ing valley south of an unnamed mountain (Mt. 1057; 53°36′N, 58°50′W; Fig. 1), and west of an unnamed lake forming the headwaters of the Eagle River (53°36′N, 58°47′W). Our total study region comprises approximately 64 km², between 500 and 1000 m in elevation. Following the terminology of Körner (2007), the timberline occurs at approximately 550 m, the treeline up to 700 m in sheltered areas, and the tree species limit at approximately 900 m. Conifer species include black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and larch (*Larix laricina* (Du Roi) K. Koch) that become increasingly stunted (i.e., krummholz) and occur in smaller, more isolated, and sheltered patches above 640 m. See Munier et al. (2010) and A.J. Trant et al. (submitted)[1] for a more complete description of the vegetation.

Bird sampling

Birds were surveyed during 2007–2008 using standard point-count methods (100 m radius; Bibby et al. 2000). Point counts were placed along transects every 300 m by following a compass bearing from an arbitrary point parallel to the trend of the valley. A total of 76 point counts were surveyed from the hours of 0400 to 1000 from 2 to 13 July 2007. During 2008, we added 38 point counts (total = 114) surveyed from 25 June to 10 July. Point counts were visited twice per season, although 12 were only surveyed once in 2007 due to logistical constraints. We attempted to minimize intra- and inter-observer reliability for bird detection. Both observers were experts with boreal songbirds, trained together to minimize inter-observer differences prior to the initiation of surveys, and had previous experience using point-count methods. Finally, we conducted point counts in a different order and by a different observer on the second visit where possible (Bibby et al. 2000). Due to safety and logistical issues associated with working in this location, point counts were conducted along routes in close proximity to one another (i.e., observers were usually approximately 300 m apart). Point counts were conducted from forest to alpine habitats between 510 and 982 m. The relatively few point counts between 760 and 900 m were largely due to very steep topography in these areas.

For each point-count site, we calculated species richness and abundance. Abundance was calculated by taking the mean number of individuals of each species for each visit (Betts et al. 2005).

The influence of detectability during avian surveys and how it varies by species, distance, and land cover is well known (Nichols et al. 2000; Rosenstock et al. 2002). However, we believe that many of these concerns were minimized in our system due to the visibility of singing and foraging birds and the simple, easily detected avifauna. Visibility was very good on most of the point-count sites due to low, well-spaced vegetation. Therefore, we believe differences in detectability among these sites should be minor. We acknowledge that more modern methods such as distance estimation (Rosenstock et al. 2002) and the double-observer approach (Nichols et al. 2000) incorporate detectability and that these methods might increase the precision of the point-count method and improve estimates of density. However, while we normally advocate the use of these methods, we believe that their utility in the studied habitat is small, for the above reasons. Methods such as spot mapping (Verner 1985) and measures like breeding productivity or nesting success (Martin and Geupel 1993) would enhance our knowledge of this system, though all of these methods are impractical in this study due to the logistical constraints of working in such a remote location.

Fig. 1. Location of the study area in the Mealy Mountains (*Akamiuapishkua*) of Labrador, Newfoundland and Labrador, Canada.
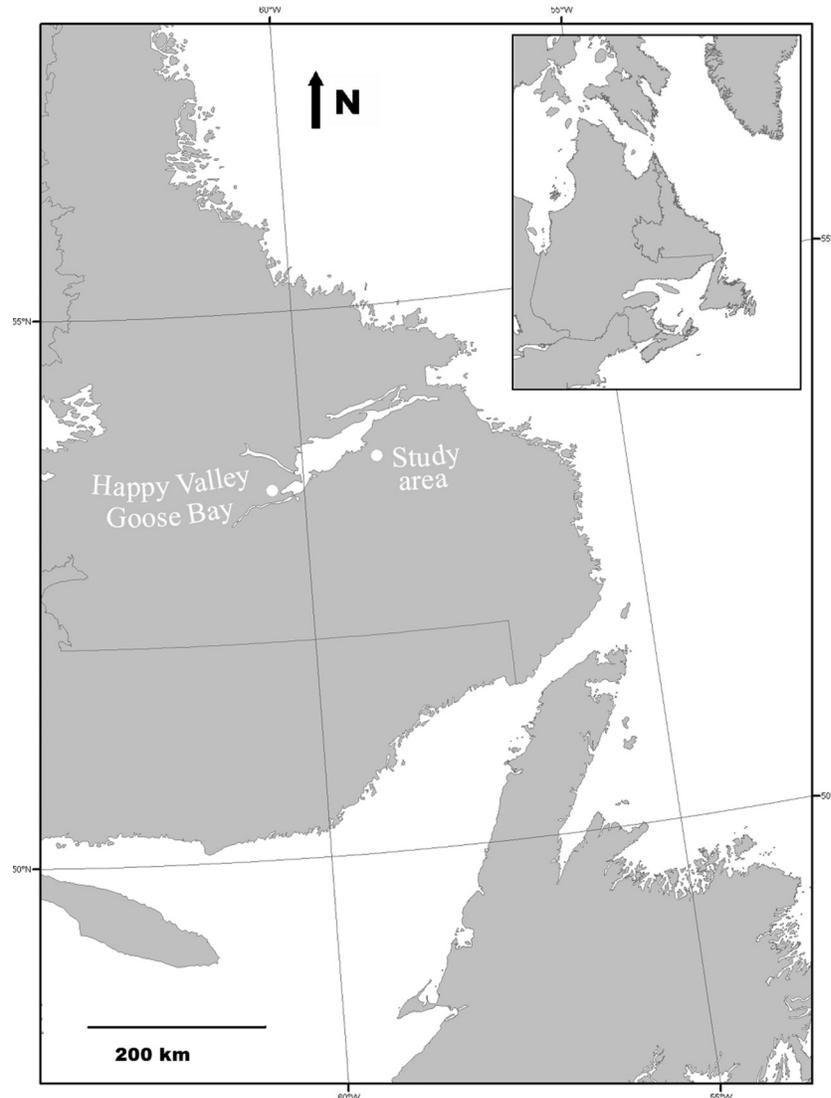
Vegetation

Because the extreme heterogeneity of the treeline ecotone and influence of glacial and other topographic features on vegetation, we used a modification of Emlen's method (Emlen 1967) to characterize vegetation on point-count circles (hereafter Emlen points; see Simon et al. 2000; Schwab et al. 2001; Simon et al. 2002). At each Emlen point, we randomly placed a 2 m pole held vertically at arm's length and classified the dominant plant species that the pole touched, as well as the surrounding habitat, based on species, plant form, and height. Emlen points were taken every 5 m on a series of transects connected in the following manner (assume that the observer is walking east–west): the observer determined a point 80 m from the centre of the circle, walked north 40 m, turned west for 20 m, and turned south for 80 m. The 20 and 80 m transects were continued a further five times, snaking across the point count and ending with a 40 m transect in a southern direction. In this way, we were able to efficiently but systematically obtain habitat classifications for all point-count circles.

On every 12th Emlen point ($n = 12$/point count), we further recorded species richness (i.e., all plant species that touched the pole) and all vegetation contacts with the pole at 0.25 m increments. We calculated the mean vegetation richness (MVR) by averaging the species richness at the 12th Emlen points per point-

count circle. As a proxy for vegetation structure, we estimated total vegetation volume (TVV; Mills et al. 1991; Fleishman et al. 2003) at each sampling point as $h/(10 \times p)$, where h is the total number of "hits" (intervals that contained vegetation) and p is the number of points at which vegetation volumes were measured. In the forest, the height of the pole was increased as was required to handle the higher vegetation layers.

Collectively, these methods allowed us to build an index of habitat types (e.g., alpine, deciduous shrub, fen, krummholz, forest, rock, late snowmelt), MVR, and TVV per point-count site, as well as a matrix of plant community composition (floristics) and vegetative height classes (physiognomy).

Analyses

Elevation strongly influences climate and vegetation and is clearly the most important determinant of vegetation in montane regions (Ruggiero and Hawkins 2008). Therefore, to control for the influence of elevation, we performed ANCOVAs with measures of avian diversity as the response variable and vegetation richness (MVR) and structure (TVV) as covariates. Point counts were divided into four broad habitat classes along an elevational gradient (i.e., alpine, deciduous shrub, krummholz, and forest) based on the data

Table 1. Elevation range of species observed on 100 m radius point counts in the Mealy Mountains, Labrador (2007 and 2008): minimum (Min.), maximum (Max.), n (number of point counts), and range (Max.–Min.).

Common name	Scientific name	Code	Mean	SD	Min.	Max.	n	Range
Red-breasted Merganser[a]	*Mergus serrator* L., 1758	RBME	683	NA	683	683	1	
Rock Ptarmigan	*Lagopus muta* (Montin, 1781)	ROPT	790	137	618	969	6	351
Willow Ptarmigan	*Lagopus lagopus* (L., 1758)	WIPT	627	55	510	740	49	230
Greater Yellowlegs[b]	*Tringa melanoleuca* (Gmelin, 1789)	GRYE	515	8	507	527	5	20
Solitary Sandpiper[b]	*Tringa solitaria* A. Wilson, 1813	SOSA	513	NA	513	513	1	
American Pipit	*Anthus rubescens* (Tunstall, 1771)	AMPI	738	96	603	982	37	379
American Robin	*Turdus migratorius* L., 1766	AMRO	609	70	507	740	67	233
American Tree Sparrow	*Spizella arborea* (A. Wilson, 1810)	AMTR	633	68	510	815	86	305
Blackpoll Warbler	*Setophaga striata* (J.R. Forster, 1772)	BLPW	584	55	503	720	78	217
Common Redpoll	*Acanthis flammea* (L., 1758)	CORE	631	89	508	982	92	474
Dark-eyed Junco	*Junco hyemalis* (L., 1758)	DEJU	568	52	507	709	53	202
Fox Sparrow	*Passerella iliaca* (Merrem, 1786)	FOSP	578	55	503	718	70	215
Gray-cheeked Thrush	*Catharus minimus* (Lafresnaye, 1848)	GCTH	529	20	503	585	23	82
Gray Jay[b]	*Perisoreus canadensis* (L., 1766)	GRJA	533	NA	533	533	1	
Horned Lark	*Eremophila alpestris* (L., 1758)	HOLA	814	110	683	982	12	299
Lincoln's Sparrow[b]	*Melospiza lincolnii* (Audubon, 1834)	LISP	595	53	503	685	26	182
Northern Shrike[b]	*Lanius borealis* Vieillot, 1808	NOSH	517	10	510	524	2	14
Northern Waterthrush	*Parkesia noveboracensis* (J.F. Gmelin, 1789)	NOWA	555	49	503	650	25	147
Pine Grosbeak[b]	*Pinicola enucleator* (L., 1758)	PIGR	524	16	503	558	8	55
Pine Siskin[b]	*Carduelis pinus* (A. Wilson 1810)	PISI	541	9	534	547	2	13
Ruby-crowned Kinglet	*Regulus calendula* (L., 1766)	RCKI	530	17	503	567	17	64
Savannah Sparrow	*Passerculus sandwichensis* (Gmelin, 1789)	SASP	590	65	510	709	15	199
Tennessee Warbler[a]	*Leiothlypis peregrina* (A. Wilson, 1811)	TEWA	551	32	510	605	10	95
Tree Swallow	*Tachycineta bicolor* (Vieillot, 1808)	TRSW	538	34	517	577	3	60
White-crowned Sparrow	*Zonotrichia leucophrys* (J.R. Forster, 1772)	WCSP	637	102	507	982	111	475
Wilson's Warbler	*Cardellina pusilla* (A. Wilson, 1811)	WIWA	567	42	503	646	43	143
White-throated Sparrow[b]	*Zonotrichia albicollis* (Gmelin, 1789)	WTSP	565	39	516	646	13	130
White-winged Crossbill[b]	*Loxia leucoptera* Gmelin, 1789	WWCR	525	17	503	560	11	57
Yellow-bellied Flycatcher[b]	*Empidonax flaviventris* (W.M. Baird and S.F. Baird, 1843)	YBFL	539	21	517	558	3	41
Yellow Warbler[a]	*Setophaga petechia* (L., 1766)	YEWA	606	30	586	641	3	55
Yellow-rumped Warbler	*Setophaga coronata* (L., 1766)	YRWA	529	21	508	605	22	97

Note: NA, not applicable.

[a]Found only in 2007.

[b]Found only in 2008.

from the Emlen points (Supplementary Table S1[2]). These classes are the most obvious features of the landscape and this division of habitat is similar to a classification of this region using remote-sensing data (Loader 2007; habitat types are a subset of these broader classes). Habitat class was included in the model as a main effect and as two-way interaction terms with the other covariates. The overall influence of a variable was assessed using the ANOVA table, but we based most of our interpretation on the coefficient estimates to determine if there was an effect of vegetation species richness or structure on avian diversity within the four habitat classes. Because deciduous shrub serves as an effective transition between treed and alpine habitats, it was used as the baseline. Years were analyzed separately. Normality of residuals, linearity, multicollinearity, and homogeneity of variance were assessed for all analyses. When computing the altitudinal range, we used observations of all birds detected at a point count.

We used nonmetric multidimensional scaling (NMDS) with fitted vectors to explore the relationships between avian species composition, habitat types (based on Emlen points), and elevation. These tests were chosen because of the large number of zeros in the species composition matrix (Oksanen et al. 2007; Zuur et al. 2007). NMDS was conducted with species regularly detected (i.e., the summed mean detections of a species across point counts per year was greater than five) within the point-count radius, e.g., Common Redpoll (*Acanthis flammea*) were often seen flying over but only rarely on the ground. After conducting the initial NMDS

analyses, we followed with analysis of similarities (ANOSIM) to quantify differences in avian communities across habitat and elevation classes. We chose three broad elevation classes, based on a combination of observations in the field and the clear separation in the NMDS itself: <700 m representing forest habitat, 700–799 m representing the forest–tundra transition, and 800+ m representing alpine habitat. We followed the ANOSIM analyses with similarity percentages (SIMPER) routines: these show the avian species responsible for the differences seen between habitat and elevation classes (Clarke and Gorley 2006). Multiple regression on distance matrices was used to assess the association between physiognomy, floristics, and avian species composition (Lichstein 2007; Robert et al. 2013).

For the linear models, we used the Rcmdr package (Fox et al. 2007) in R (R Development Core Team 2007). NMDS were conducted using package "vegan", the former using function "metaMDS" (Oksanen et al. 2007) in R. PRIMER v6 (Clarke and Gorley 2006) was also used to conduct NMDS, as well as ANOSIM and SIMPER. To evaluate the relationship between the dominant vegetative types and the avian species ordination, we used the function "envfit" in R. Envfit calculates vectors that maximize the correlation between ordination scores and habitat variables. A goodness-of-fit statistic (r^2) was computed for each vector by calculating 1000 random permutations of the maximum correlation between NMDS ordination scores and habitat variables (Oksanen et al. 2007). Multiple regres-

Table 2. Avian species richness and abundance, as well as vegetation species richness and total vegetation volume, by habitat type.

Habitat type	Avian species richness		Avian abundance		Vegetation species richness	Total vegetation volume
	2007	2008	2007	2008		
Alpine	2.2±0.9	3.0±1.3	4.3±2.3	4.8±2.4	1.0±0.4	0.7±0.5
Deciduous shrub	3.2±1.1	3.4±1.2	5.5±2.3	5.6±1.8	0.9±0.4	0.6±0.5
Krummholz	3.4±0.9	3.8±1.2	6.0±1.7	5.8±2.0	1.1±0.3	1.0±0.4
Forest	4.4±0.7	6.0±1.7	8.5±1.8	8.6±3.1	1.4±0.5	1.4±0.7
Total	3.1±1.2	4.0±1.8	5.6±2.4	6.2±2.8	1.1±0.4	0.9±0.6

Note: Avian values are presented by year. Values are means ± SD.

Fig. 2. Nonmetric multidimensional scaling (NMDS) plot of bird community composition by elevation in the Mealy Mountains (*Akamiuapishkua*), Labrador, for the year 2008. BinElev includes the bird community in the 50 m including and above the stated value (e.g., 800 = 800–849 m).
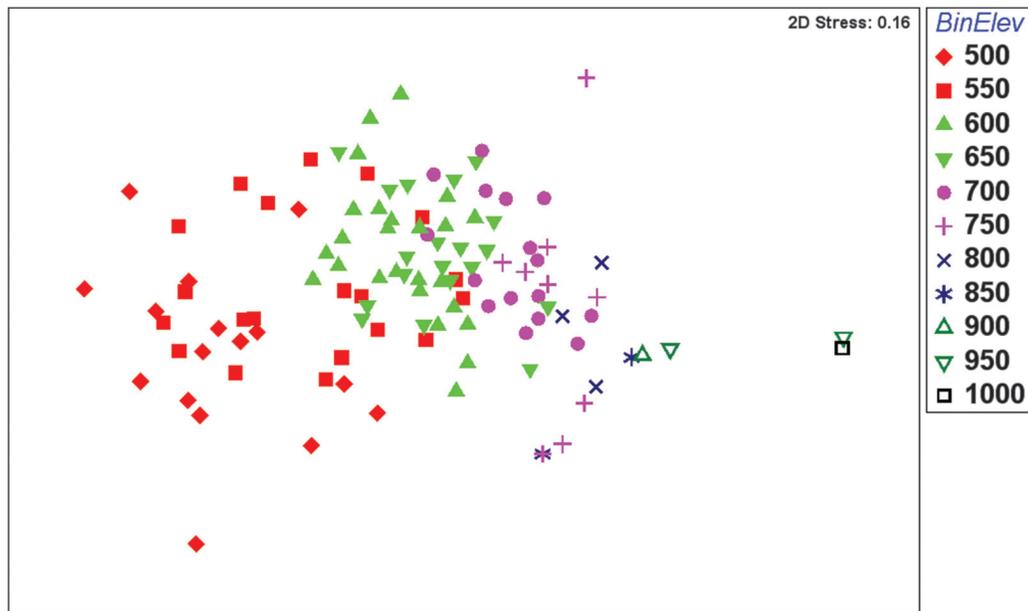
sion on distance matrices was performed using package "ecodist" (Goslee and Urban 2007) in R.

Results

Bird and vegetation community composition

In 2007, we observed 763 individuals and 15 bird species, while in 2008, we observed 1369 individuals and 24 bird species. Common Redpoll and White-crowned Sparrow (*Zonotrichia leucophrys*) were the most widespread and ubiquitous species in both years and were found over a 470 m range in elevation (Table 1). Willow Ptarmigan (*Lagopus lagopus*) was the only abundant nonpasserine species.

We observed 65 different categories of plants and ground cover. These included 46 plant species and 9 genera or higher taxa (e.g., sphagnum mosses). Other categories included water, rock, and leaf litter. MVR differed significantly among habitat classes ($F_{[3,110]} = 11.6$, $p < 0.0001$). MVR did not differ between alpine and deciduous shrub but was significantly greater in forest and krummholz than in deciduous shrub (forest and deciduous shrub: $t_{[110]} = 5.5$, $p < 0.0001$; krummholz and deciduous shrub: $t_{[110]} = 2.2$, $p = 0.03$). Overall, TVV differed significantly among habitat classes ($F_{[3,110]} = 31.43$, $p < 0.0001$). Specifically, TVV did not differ between alpine and deciduous shrub, but was significantly higher in forest ($t_{[110]} = 8.7$, $p < 0.0001$) and krummholz ($t_{[110]} = 2.9$, $p < 0.005$; Table 2).

Bird–vegetation relationships

Diversity

Elevation plays a strong role in determining avian community composition (Fig. 2). Multivariate tests showed a strong difference in avian community structure with elevation (ANOSIM, global $R = 0.326$, $p = 0.001$), with the avian community of each elevation differing from each of the other elevation classes (Supplementary Table S2).[2] This difference was driven to a large extent by forest generalist bird species (e.g., AMRO, BLPW) declining with elevation (SIMPER: Supplementary Table S3[2] and below). Richness and abundance were generally highest in the forest but similar in the other habitat types.

Overall, avian richness increased with MVR ($F_{[1,102]} = 5.09$, $p = 0.026$), TVV ($F_{[1,102]} = 7.03$, $p = 0.009$), and among habitat classes ($F_{[3,102]} = 6.5$, $p = 0.005$) in 2008. Within each habitat class, richness did not significantly change with MVR but increased with TVV ($t_{[102]} = 2.7$, $p = 0.009$ for deciduous shrub); slopes for other habitat classes did not differ from deciduous shrub (Fig. 3). Avian richness was significantly higher in the forest compared with other habitats ($t_{[102]} = 2.85$, $p = 0.006$). In 2007, the richness did not differ with MVR and TVV but did by habitat class ($F_{[3,64]} = 3.34$, $p = 0.03$). Richness was significantly lower in alpine than in deciduous shrubs ($t_{[64]} = -2.25$, $p = 0.03$; Table 2).

Avian abundance increased with MVR ($F_{[1,102]} = 15.26$, $p = 0.0002$) and TVV ($F_{[1,102]} = 12.18$, $p = 0.0007$) in 2008; these increases were consistent across habitat class. Although the overall term was not

Fig. 3. Influence of total vegetation volume (m³/m²) on bird species richness in 2008 in four habitat types. The regression lines for each habitat (broken lines) and overall regression line (solid line) are shown. Box-and-whisker plots denote the spread of the variable along the axis.
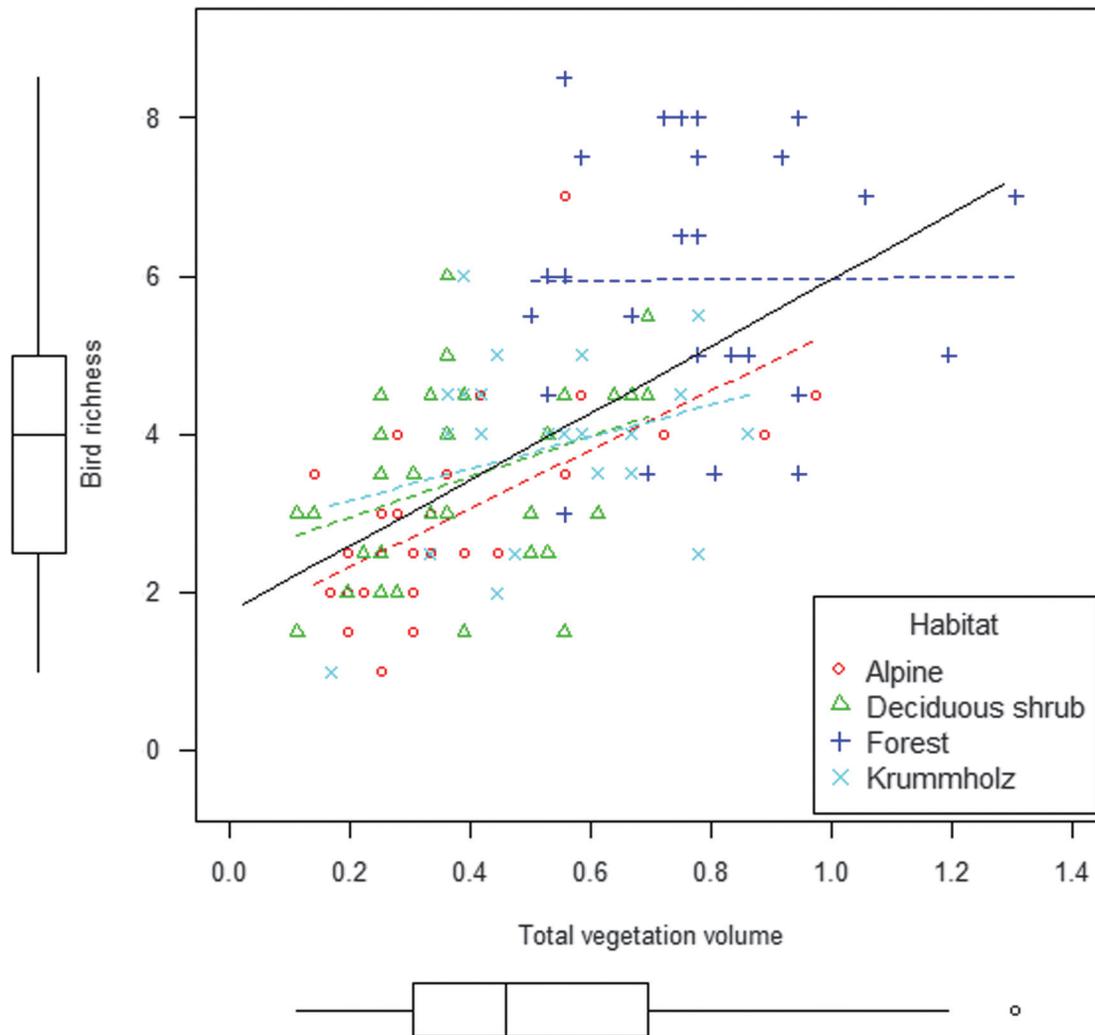
significant ($F_{[3,102]}$ = 1.8, p = 0.15), abundance in 2008 was significantly higher in the forest compared with other habitat classes ($t_{[102]}$ = 2.4, p = 0.018). In 2007, none of the explanatory variables or coefficients was significant (Table 2).

Composition

The correlation of the avian species distribution with the habitat variables is summarized in Figs. 4A and 4B. Results were largely consistent between years for the 17 types of habitat that we identified, with most of the major habitat type or avian assemblage correlations conserved (Table 3). Alder (genus *Alnus* Mill.), late snowmelt areas, willow (genus *Salix* L.), scrub spruce, and water (i.e., ponds) habitats were not significantly correlated with the avian assemblage in either year. Fen and krummholz forest were not significantly correlated with the avian assemblage in 2007. Elevation was the most robust variable explaining much of the variance in both years.

Habitat associations are typical of most species and are generally consistent among years (Figs. 4A and 4B). American Pipit (*Anthus rubescens*) was strongly associated with elevation and also alpine. The abundances of American Tree Sparrow and Willow Ptarmigan were strongly correlated with deciduous shrub and krummholz. Lincoln's Sparrow (*Melospiza lincolnii*) and American Robin (*Turdus migratorius*) were correlated with krummholz. Many species, such as Gray-cheeked Thrush (*Catharus minimus*) and Yellow-

rumped Warbler (*Setophaga coronata*), were strongly correlated with forest habitat, especially in 2008. Some species such as Blackpoll Warbler (*Setophaga striata*) were not strongly associated with any habitat but were negatively correlated with elevation and alpine. White-crowned Sparrow was weakly correlated with rock and alpine habitats in 2008 but strongly correlated with forest in 2007. This discrepancy is likely due to the large elevational range of this species and differences in sample sizes between years.

The association between vegetation and avian species composition varied with habitat class. Avian species composition was correlated with physiognomy on alpine sites and deciduous shrub site and with floristics on alpine sites in 2007 (Table 4). There were no significant correlations between avian composition, floristics, or physiognomy in krummholz or forest habitat in either year.

Discussion

Elevation and its subsequent impact on vegetation is the strongest driver of species composition across the treeline ecotone. This trend was reflected in the difference in avian richness among habitat classes and a strong negative relationship with avian composition (Figs. 2, 4A, and 4B).

Although many studies have examined avian diversity in relation to elevation, these studies are usually conducted from a biogeographic perspective, concerned with testing hypotheses that

Fig. 4. A two-dimensional, nonmetric multidimensional scaling (NMDS) ordination of species scores for (A) 2007 and (B) 2008 (see Table 2). Stress <0.15 for both years. The + signs indicate the location of the species scores. Codes for bird species and habitat types are in Tables 1 and 3, respectively. "Envfit" was used to create and overlay vectors on the ordination. For clarity, only vectors with *p* < 0.01 in 2007 and *p* < 0.006 in 2008 are shown.
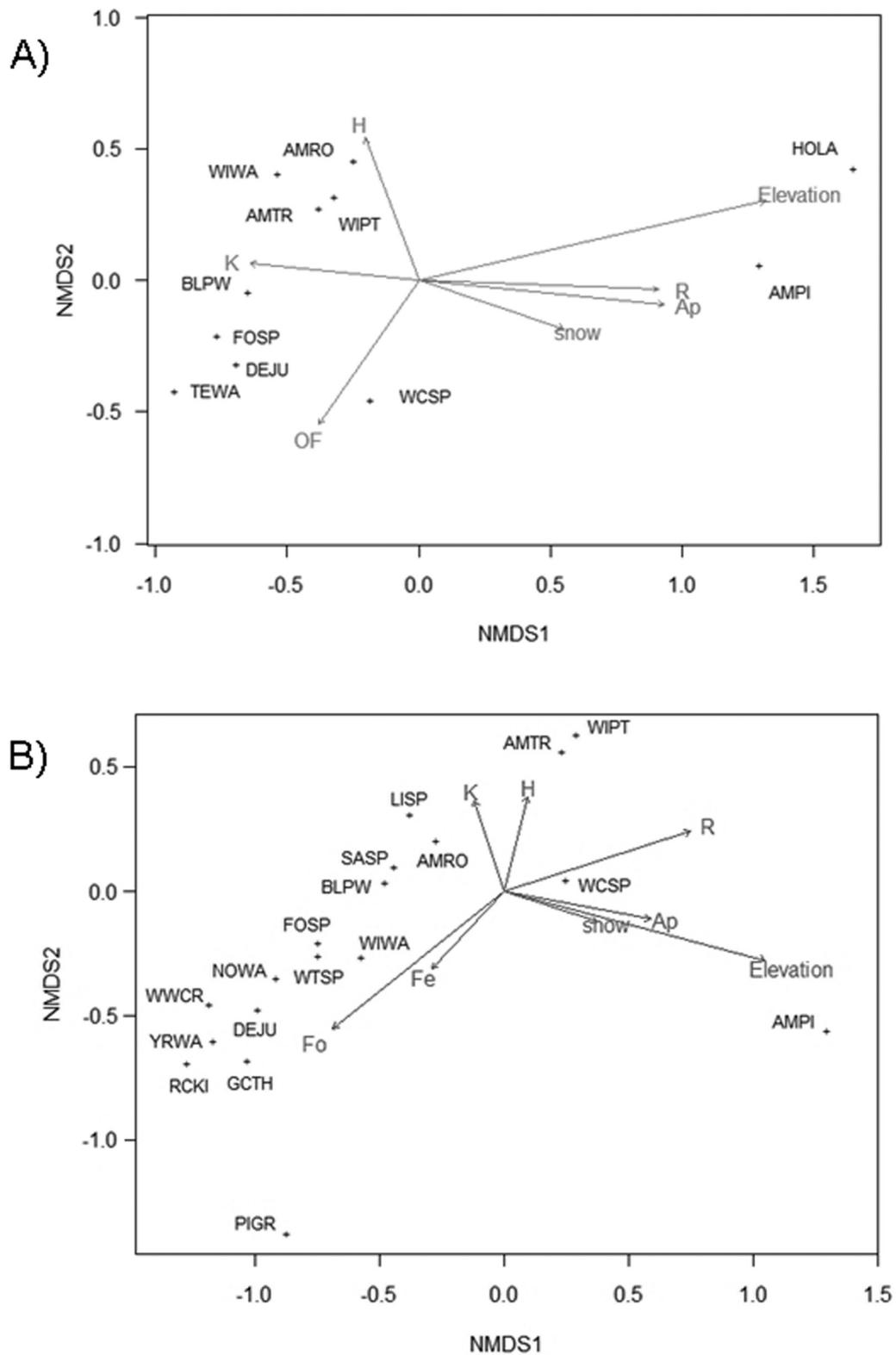
explain species richness over long elevational gradients (e.g., Herzog et al. 2005; Ruggiero and Hawkins 2008). These studies do not examine the vegetation–habitat concept nor do they explicitly examine ecotones. Other studies have examined these concepts, but this is the first study, to the best of our knowledge, to do so across a boreal treeline ecotone (see Terborgh 1985; Archaux 2004; Lloyd et al. 2011; Kent et al. 2013 for nonboreal treeline examples) and to consider the potential impacts of global climate change (see Conservation impli-

Table 3. Squared correlation coefficients (r^2) and significance levels (based on 1000 random permutations of the data) of habitat types with the avian assemblages based on the nonmetric multidimensional scaling (NMDS) in 2007 and 2008.

	2007		2008	
	r^2	p	r^2	p
Alder (Ad)	0.08	0.05	0.01	0.51
Alpine (Ap)	0.37	<0.001***	0.23	<0.001***
Fen (Fe)	0.01	0.83	0.12	0.002**
Forest (Fo)	0.09	0.03*	0.50	<0.001***
Deciduous shrub (H)	0.14	0.01**	0.10	<0.001***
Krummholz (K)	0.18	<0.001***	0.10	0.006**
Krummholz forest (KF)	0.05	0.14	0.06	0.04*
Late snowmelt (LS)	0.01	0.70	0.01	0.67
Open Forest (OF)	0.19	<0.001***	0.09	0.009**
Rock (R)	0.36	<0.001***	0.40	<0.001***
Salix	0.01	0.62	0.01	0.59
Sedge (Se)	0.07	0.09	0.02	0.29
Snow	0.14	<0.01***	0.10	0.003**
Scrub spruce (SS)			0.04	0.08
Stream (STR)	0.00	0.90	0.01	0.51
Water (W)	0.06	0.12	0.02	0.41
Elevation	0.78	<0.001***	0.76	<0.001***

Note: Habitat variables are independently modeled. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

cations below, but also Cumming et al. 2014). Furthermore, while we are in general agreement with Cumming et al. (2014) that most studies of boreal song birds occur over too small a spatial extent to detect the influence of climate variation, ecotone studies ameliorate this to a large degree. Indeed one of the strengths of this study is the documented change in climate (Jacobs et al. 2014), vegetation (A.J. Trant et al., submitted[1]), and avian composition over the short elevational gradient.

Ecotones

Avian diversity did not increase across the ecotone but was highest in the forest (Figs. 4A and 4B, Table 2, Supplementary Table S3[2]), likely because of the increase in nesting and foraging opportunities. Furthermore, while some species were clearly associated with the treeline (Figs. 4A and 4B), similar to Lloyd et al. (2011), they are clearly not treeline specialists. The birds in this study are all quite common across North America (e.g., American Robin), and the ecotone is far too narrow in these mountains to promote speciation; in all likelihood, these birds were simply using the area along the elevational gradient with their preferred floristics and physiognomy. Simple relationships have been hypothesized for the influence of ecotones including increased diversity (Odum 1958), but further study has often produced little consensus because the relationship is far more complex than originally realized (Murcia 1995; Baker et al. 2002).

Bird–vegetation relationships

Diversity and composition

Overall, richness and abundance generally increased with MVR) and TVV; Fig. 3). The result of TVV, but not MVR, being associated with avian diversity is consistent with Fleishman et al. (2003). The discrepancies between 2007 and 2008, i.e., nonsignificant as opposed to significant findings, respectively, are likely due to the low number of point counts and lesser coverage in some habitat types in 2007.

As with measures of diversity, elevation is the most robust predictor of avian composition. However, elevation is just a surrogate for other variables; it does not control avian composition per se. Most species correlate well with one or two of the dominant habitat types, justifying our division into habitat class (Table 3, Figs. 4A and 4B). Those few that do not can be considered habitat

generalists, like the American Robin, found from forest to deciduous shrub, and the White-crowned Sparrow, found from the timberline to alpine. Discrepancies between years in correlation coefficients for fen and forest (Table 3) are likely due to the greater number of species detected in 2008 and their association with these habitat types (Table 1, Figs. 4A and 4B).

This is the first study of avian diversity in the highlands of Labrador and of highlands of eastern Canada in general. Although a number of avian studies have been conducted in the boreal forests of Labrador (Simon et al. 2000, 2002; Schwab et al. 2001) and Quebec (Imbeau et al. 1999), as well as the low Arctic of Quebec (Andres 2006), these studies have largely been focused on forests and forestry issues. Abundance, type, and diversity of species were similar to results from these studies. Although these studies were not conducted near the treeline, many of them occurred on burned, clearcut, or early successional plots. Abundances of White-crowned Sparrows and White-throated Sparrows (*Zonotrichia albicollis*) were highest in these habitats and are likely to be structurally similar to our deciduous shrub and krummholz sites. However, there were some differences. American Pipit (*Anthus rubescens*), Horned Lark (*Eremophila alpestris*), Savannah Sparrow (*Passerculus sandwichensis*), and Rock Ptarmigan (*Lagopus muta*) are not reported in the abovementioned Labrador studies because they are found almost strictly above the treeline. We also found Grey-cheeked Thrush rather than Hermit Thrush (*Catharus guttatus* (Pallas, 1811)) and Swainson's Thrush (*Catharus ustulatus* (Nuttall, 1840)). We suggest that this is due to the dense woody undergrowth and alder thickets in these higher elevation forests that Gray-cheeked Thrush favour (Lowther et al. 2001). We note here that Rock Ptarmigan, known to occur in northern Labrador, have not been reported breeding in this area before, and this southern outlier of a more northern species may be expected to be lost as treeline advances over alpine habitat (Montgomerie and Holder 2008).

Results of the multiple regression on distance matrices were not consistent with Rotenberry's hypothesis that floristics are more important for avian assemblages within a habitat (Table 4; Rotenberry 1985; Bersier and Meyer 1994; Fleishman et al. 2003; Lee and Rotenberry 2005 and references therein). In alpine and deciduous shrub habitats, with the exception of 2007, the results were opposite. One explanation for this finding is that bare rock is a significant feature in alpine habitat and to a lesser degree in deciduous shrub habitat. Rock clearly does not contribute to the physiognomy of the system. This suggests that some vegetation structure is better than none at all and that physiognomy is more important than floristics. In addition, some small, isolated krummholz stands were found in areas that are predominantly shrub habitat and this may have a similar effect. Other studies have found a similar pattern (Shahabuddin and Kumar 2007), which is more consistent with the original hypotheses that avian diversity is more strongly correlated with vegetation habitat diversity rather than vegetation species (MacArthur et al. 1962). However, avian diversity studies beyond the treeline ecotone are rare and similarity between alpine and other habitat classes is low, suggesting that these species respond to vegetation in different ways than others (Catsadorakis 1997). In many places, alpine habitat is predicted to be lost with changing climate (Rosenzweig et al. 2007).

Our results were inconclusive for Rotenberry's hypothesis in krummholz and forest habitats. Krummholz habitat contains stunted spruce and balsam fir trees that form dense patches on the landscape, much different in structure than the vegetation either higher in elevation (alpine tundra) or lower (open canopy forest). It is not clear why changes in floristics and physiognomy were not associated with avian composition in krummholz, but there are two possible explanations. First, birds may be responding to other habitat features within this zone (Knick et al. 2008). Krummholz were simply the dominant vegetation in a transition zone from relatively unbroken forest to deciduous shrub with a few tree-islands to treeless alpine habitat. The krummholz zone

Table 4. Multiple regression on distance matrices between avian species composition, vegetation species composition (floristics; mean vegetation richness (MVR)), and vegetation structure (physiognomy; total vegetation volume (TVV)).

Coefficient	Alpine		Deciduous shrub		Krummholz		Forest	
	2007	2008	2007	2008	2007	2008	2007	2008
MVR	**0.34, 0.03**	0.05, 0.67	0.01, 0.41	0.02, 0.82	0.06, 0.71	0.14, 0.29	−0.12, 0.74	−0.11, 0.44
TVV	**0.23, 0.01**	**0.25, <0.01**	**0.14, 0.01**	**0.14, <0.01**	−0.05, 0.74	0.22, 0.05	−0.27, 0.15	0.14, 0.20

Note: Results are given as the regression coefficients and *p* values (significant values are set in boldface type).

forms a very fragmented, narrow band across the ecotonal gradient between forest and alpine habitat types and is often embedded within a matrix of secondary habitat types (late snowmelt areas, fen, streams). Alternately, Norment (1991) found that avian diversity in the subalpine forest–alpine tundra ecotone was positively correlated with forest patch size and edge, though we are unable to test for this in our system. It is possible that this latter explanation accounts for the lack of correlation of avian composition and vegetation in the forest habitat. As with most ecological patterns, multiple factors structure avian communities.

Conservation implications

This is the first study to examine avian communities at a treeline in Labrador. There are two general hypotheses for how treeline may change with climate change: (1) infilling of presently patchy habitat and (2) general advance of the leading edge of treeline, both poleward and upward in elevation (Danby and Hik 2007). In the infilling scenario, physiognomy changes dramatically, but floristics may not. In the advance scenario, both physiognomy and floristics may change as treeline advances. Each scenario will have different impacts on local and regional avian communities. In an infilling scenario, alpine and shrub habitats may not decrease in area, leading to maintenance of the habitat for alpine- and shrub-associated species. In general, the regional community will not change, but some species may fare poorly such as the Blackpoll Warbler and American Robin that do well in patchy tree–shrub habitats. In the advance scenario, alpine and shrub habitats may be lost, with little change in the proportion of below treeline habitat (Danby and Hik 2007). This may lead to important local and regional changes in communities of birds found above the treeline: alpine species such as the American Pipit, Horned Lark, and Rock Ptarmigan would be lost, eliminating these southern outposts of more northerly species.

Conclusion

We examined the impact of elevation, as well as floristics and physiognomy of vegetation, on avian communities across a treeline ecotone in the Mealy Mountains, Labrador, Canada. Our findings suggest that elevation plays a strong role in structuring avian communities and are generally inconsistent with the vegetation–habitat concept, i.e., that birds are influenced by vegetation structure and by composition at more local scales. Given the strong impact of elevation on vegetation structure and avian communities, we note that for bird species whose near-southernmost populations are found in the Mealy Mountains, climate change is likely to have a strong negative effect as alpine tundra habitat is lost. Furthermore, forest-associated species are likely to benefit from the increased tree cover as treeline moves poleward and upward.

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References

Andres, B.A. 2006. An arctic-breeding bird survey on the northwestern Ungava Peninsula, Quebec, Canada. Arctic, **59**: 311–318. doi:10.14430/arctic316.

Archaux, F. 2004. Breeding upwards when climate is becoming warmer: no bird response in the French Alps. Ibis, **146**: 138–144. doi:10.1111/j.1474-919X.2004.00246.x.

Baker, J., French, K., and Whelan, R.J. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology, **83**: 3048–3059. doi:10.1890/0012-9658(2002)083[3048:TEEAES]2.0.CO;2.

Bell, T., Jacobs, J.D., Munier, A., Leblanck, P., and Trant, A. 2008. Climate change and renewable resources in Labrador: looking toward 2050. *In* Proceedings and Report of a Conference held in North West River, Labrador, 11–13 March 2008. Labrador Highlands Research Group, Memorial University of Newfoundland, St. John's.

Bersier, L.-F., and Meyer, D.R. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecol. **15**: 561–576.

Betts, M.G., Simon, N.P.P., and Nocera, J.J. 2005. Point count summary statistics differentially predict reproductive activity in bird–habitat relationship studies. J. Ornithol. **146**: 151–159. doi:10.1007/s10336-005-0074-9.

Bibby, C.J., Burgess, N.D., Hill, D.A., and Mustoe, S.H. 2000. Bird census techniques. 2nd ed. Academic Press, London.

Blancher, P.J. 2003. Importance of Canada's boreal forest to landbirds. Canadian Boreal Initiative, Ottawa, Ont., and Boreal Songbird Initiative, Seattle, Wash.

Blancher, P.J., and Wells, J. 2005. The boreal forest region: North America's bird nursery. Canadian Boreal Initiative, Ottawa, Ont., and Boreal Songbird Initiative, Seattle, Wash.

Cannone, N., Sgorbati, S., and Guglielmin, M. 2007. Unexpected impacts of climate change on alpine vegetation. Front. Ecol. Environ. **5**: 360–364. doi:10.1890/1540-9295(2007)5[360:UIOCCO]2.0.CO;2.

Catsadorakis, G. 1997. Breeding birds from reedbeds to alpine meadows. Hydrobiologia, **351**: 143–155. doi:10.1023/A:1003080911744.

Clarke, K.R., and Gorley, R.N. 2006. PRIMER v6: user manual/tutorial. PRIMER-E Ltd., Plymouth, UK.

Cody, M.L. 1985. Habitat selection in birds. Academic Press, San Diego, Calif.

Cumming, S.G., Stralberg, D., Lefevre, K.L., Sólymos, P., Bayne, E.M., Fang, S., Fontaine, T., Mazerolle, D., Schmiegelow, F.K.A., and Song, S.J. 2014. Climate and vegetation hierarchically structure patterns of songbird distribution in the Canadian boreal region. Ecography, **37**: 137–151. doi:10.1111/j.1600-0587.2013.00299.x.

Danby, R.K., and Hik, D.S. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. J. Ecol. **95**: 352–363. doi:10.1111/j.1365-2745.2006.01200.x.

Emlen, J.T. 1967. A rapid method for measuring arboreal canopy cover. Ecology, **48**: 158–159. doi:10.2307/1933429.

Fleishman, E., Mcdonal, N., Mac Nally, R., Murphy, D.D., Walters, J., and Floyd, T. 2003. Effects of floristics, physiognomy and non-native vegetation on riparian bird communities in a Mojave Desert watershed. J. Anim. Ecol. **72**: 484–490. doi:10.1046/j.1365-2656.2003.00718.x.

Fox, J., with contributions from Ash, M., Boye, T., Calza, S., Chang, A., Grosjean, P., Heiberger, R., Kerns, G.J., Lancelot, R., Lesnoff, M., Messad, S., Maechler, M., Neuwirth, E., Putler, D., Ristic, M., and Wolf, P. 2007. Rcmdr: R Commander. R package version 1.3-5 [computer programs]. Available from http://www.r-project.org and http://socserv.socsci.mcmaster.ca/jfox/Misc/Rcmdr/.

Goslee, S.C., and Urban, D.L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. **22**: 1–19.

Grace, J., Berninger, F., and Nagy, L. 2002. Impacts of climate change on the tree line. Ann. Bot. **90**: 537–544. doi:10.1093/aob/mcf222. PMID:12324278.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., and Esseen, P.-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. **19**: 768–782. doi:10.1111/j.1523-1739.2005.00045.x.

Harper, K.A., Danby, R.K., De, Fields, D.L., Lewis, K.P., Trant, A.J., Starzomski, B.M., Savidge, R., and Hermanutz, L. 2011. Tree spatial pattern

within the forest–tundra ecotone: a comparison of sites across Canada. Can. J. For. Res. 41(3): 479–489. doi:10.1139/X10-221.

Harsch, M.A., Hulme, P.E., McGlone, M.S., and Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol. Lett. 12: 1040–1049. PMID:19682007.

Herzog, S.K., Kessler, M., and Bach, K. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. Ecography, 28: 209–222. doi:10.1111/j.0906-7590.2005.03935.x.

Imbeau, L., Savard, J.-P.L., and Gagnon, R. 1999. Comparing bird assemblages in successional black spruce stands originating from fire and logging. Can. J. Zool. 77(12): 1850–1860. doi:10.1139/z99-172.

Jacobs, J.D., Chan, S., and Sutton, E. 2014. Climatology of the forest–tundra ecotone at a Maritime Subarctic–Alpine Site, Mealy Mountains, Labrador. Arctic, 67: 28–42. doi:10.14430/arctic4358.

James, F.C., and Wamer, N.O. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology, 63: 159–171. doi:10.2307/1937041.

Kent, R., Levanoni, O., Banker, E., Pe'er, G., and Kark, S. 2013. Comparing the response of birds and butterflies to vegetation-based mountain ecotones using boundary detection approaches. PloS ONE, 8: e58229. doi:10.1371/journal.pone.0058229.

Knick, S.T., Rotenberry, J.T., and Leu, M. 2008. Habitat, topographical, and geographical components structuring shrubsteppe bird communities. Ecography, 31: 389–400. doi:10.1111/j.0906-7590.2008.05391.x.

Körner, C. 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22: 569–574. doi:10.1016/j.tree.2007.09.006. PMID:17988759.

Lee, P., and Rotenberry, J.T. 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. J. Biogeogr. 32: 1139–1150. doi:10.1111/j.1365-2699.2005.01254.x.

Lichstein, J.W. 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188: 177–131. doi:10.1007/s11258-006-9126-3.

Lloyd, H., Ríos, S.S., Marsden, S.J., and Valdés-Velásquez, A. 2011. Bird community composition across an Andean tree-line ecotone. Austral Ecol. 37: 470–478.

Loader, S. 2007. Spatially explicit modeling of topographic and climatic influences on vegetation distribution in Labrador's Mealy Mountains. M.Sc. thesis, Memorial University of Newfoundland, St. John's.

Lowther, P.E., Rimmer, C.C., Kessel, B., Johnson, S.L., and Ellison, W.G. 2001. Gray-cheeked Thrush (Catharus minimus). In The Birds of North America Online. Edited by A. Poole. Cornell Lab of Ornithology, Ithaca, N.Y. doi:10.2173/bna.591.

MacArthur, R.H., MacArthur, J.W., and Preer, J. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. Am. Nat. 96: 167–174. doi:10.1086/282219.

Martin, T.E., and Geupel, G.R. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. J. Field Ornithol. 64: 507–519.

Meades, S.J. 1990. Natural regions of Newfoundland and Labrador. Protected Areas Association, St. John's.

Mills, G.S., Dunning, J.B., Jr., and Bates, J.M. 1991. The relationship between breeding bird density and vegetation volume. Wilson Bull. 103: 468–479.

Montgomerie, R., and Holder, K. 2008. Rock Ptarmigan (Lagopus muta). In The Birds of North America Online. Edited by A. Poole. Cornell Lab of Ornithology, Ithaca, N.Y. doi:10.2173/bna.51.

Munier, A., Hermanutz, L., Jacobs, J.D., and Lewis, K.P. 2010. The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. Plant Ecol. 210: 19–30. doi:10.1007/s11258-010-9724-y.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10: 58–62. doi:10.1016/S0169-5347(00)88977-6. PMID:21236953.

Nichols, J.D., Hines, J.E., Sauer, J.R., Fallon, F.W., Fallon, J.E., and Heglund, P.J. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk, 117: 393–408. doi:10.2307/4089721.

Norment, C.J. 1991. Bird use of forest patches in the subalpine forest–alpine tundra ecotone of the Beartooth Mountains, Wyoming. Northwest Sci. 65: 1–9.

Odum, E.P. 1958. Fundamentals of ecology. 2nd ed. Saunders, Philadelphia, Pa.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Henry, M., and Stevens, H. 2007. vegan: community ecology package. R package version 1.8-8 [computer program]. Available from http://cran.r-project.org/web/packages/vegan/index.html.

Payette, S., Fortin, M.-J., and Gamache, I. 2001. The subarctic forest–tundra: the structure of a biome in a changing climate. BioScience, 51: 709–718. doi:10.1641/0006-3568(2001)051[0709:TSFTTS]2.0.CO;2.

R Development Core Team 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org.

Ries, L., and Sisk, T.D. 2004. A predictive model of edge effects. Ecology, 85: 2917–2926. doi:10.1890/03-8021.

Risser, P.G. 1995. The status of the science examining ecotones. BioScience, 45: 318–325. doi:10.2307/1312492.

Robert, K., Garant, D., Vander Wal, E., and Pelletier, F. 2013. Context-dependent social behaviour: testing the interplay between season and kinship with raccoons. J. Zool. (Lond.), 290: 199–207. doi:10.1111/jzo.12027.

Rosenstock, S.S., Anderson, D.R., Giesen, K.M., Leukering, T., and Carter, M.F. 2002. Landbird counting techniques: current practices and an alternative. Auk, 119: 46–53. doi:10.1642/0004-8038(2002)119[0046:LCTCPA]2.0.CO;2.

Rotenberry, J.T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia, 67: 213–217. doi:10.1007/BF00384286.

Rosenzweig, C., Casassa, G., Karoly, D.J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T.L., Seguin, B., and Tryjanowski. P. 2007. Assessment of observed changes and responses in natural and managed systems. In Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson. Cambridge University Press, Cambridge, UK. pp. 79–131.

Ruckstuhl, K.E., Johnson, E.A., and Miyanishi, K. 2008. Introduction: The boreal forest and global change. Philos. Trans. R. Soc. B Biol. Sci. 363: 2243–2247. doi:10.1098/rstb.2007.2196.

Ruggiero, A., and Hawkins, B.A. 2008. Why do mountains support so many species of birds? Ecography, 31: 306–315. doi:10.1111/j.0906-7590.2008.05333.x.

Schwab, F.E., Simon, N.P.P., and Carroll, C.G. 2001. Breeding songbird abundance related to secondary succession in the subarctic forests of western Labrador. Ecoscience, 8: 1–7.

Shahabuddin, G., and Kumar, R. 2007. Effects of extractive disturbance on bird assemblages, vegetation structure and floristics in tropical scrub forest, Sariska Tiger Reserve, India. For. Ecol. Manage. 246: 175–185. doi:10.1016/j.foreco.2007.03.061.

Simon, N.P.P., Schwab, F.E., and Diamond, A.W. 2000. Patterns of breeding bird abundance in relation to logging in western Labrador. Can. J. For. Res. 30(2): 257–263. doi:10.1139/x99-203.

Simon, N.P.P., Schwab, F.E., and Otto, R.D. 2002. Songbird abundance in clear-cut and burned stands: a comparison of natural disturbance and forest management. Can. J. For. Res. 32(8): 1343–1350. doi:10.1139/x02-057.

Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. Ecology, 66: 1237–1246. doi:10.2307/1939177.

Verner, J. 1985. Assessment of counting techniques. Curr. Ornithol. 2: 247–302.

Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007. Analysing ecological data. Springer-Verlag, New York.